

This article was downloaded by: [National Agricultural Library]

On: 1 June 2010

Access details: Access Details: [subscription number 917355782]

Publisher Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



## Journal of Crop Improvement

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t792303981>

## Photosynthesis, Growth, and Yield of Citrus at Elevated Atmospheric CO<sub>2</sub>

Joseph C. V. Vu<sup>ab</sup>

<sup>a</sup> Crop Genetics and Environmental Research Unit, U.S. Department of Agriculture-Agricultural Research Service, USA <sup>b</sup> Agronomy Department, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL, USA

**To cite this Article** Vu, Joseph C. V.(2005) 'Photosynthesis, Growth, and Yield of Citrus at Elevated Atmospheric CO<sub>2</sub>', Journal of Crop Improvement, 13: 1, 361 — 376

**To link to this Article:** DOI: 10.1300/J411v13n01\_17

**URL:** [http://dx.doi.org/10.1300/J411v13n01\\_17](http://dx.doi.org/10.1300/J411v13n01_17)

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.informaworld.com/terms-and-conditions-of-access.pdf>

This article may be used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

# Photosynthesis, Growth, and Yield of Citrus at Elevated Atmospheric CO<sub>2</sub>

Joseph C. V. Vu

**SUMMARY.** Agricultural productivity is expected to be affected by rising atmospheric carbon dioxide concentration ([CO<sub>2</sub>]) and changing climate. Increase in [CO<sub>2</sub>] *per se* may lead to higher yield for several crop species, including citrus. However, the interactions between elevated [CO<sub>2</sub>] and other climatic change factors are complex, and producing crops under global climate changes will be a challenge for world agriculture. This review focuses on our current understanding of citrus photosynthesis, growth, and yield in response to rising atmospheric [CO<sub>2</sub>]. There is indeed a critical need to unravel the mechanisms of citrus responses to atmospheric [CO<sub>2</sub>] enrichment and climate changes, and to identify the targets for a genetic/breeding approach designed to enhance citrus tolerance/resistance to environmental stresses. [Article copies available for a fee from The Haworth Document Delivery Service: 1-800-HAWORTH. E-mail address: <docdelivery@haworthpress.com> Website: <<http://www.HaworthPress.com>> © 2005 by The Haworth Press, Inc. All rights reserved.]

**KEYWORDS.** Rising atmospheric CO<sub>2</sub>, global climate change, citrus, photosynthesis, yield

---

Joseph C. V. Vu is Research Plant Physiologist, Crop Genetics and Environmental Research Unit, U.S. Department of Agriculture-Agricultural Research Service, and Professor, Agronomy Department, Institute of Food and Agricultural Sciences, 304 Newell Hall, P.O. Box 110500, University of Florida, Gainesville, FL 32611-0500 USA (E-mail: jcvu@mail.ifas.ufl.edu).

[Haworth co-indexing entry note]: "Photosynthesis, Growth, and Yield of Citrus at Elevated Atmospheric CO<sub>2</sub>." Vu, Joseph C. V. Co-published simultaneously in *Journal of Crop Improvement* (Food Products Press, an imprint of The Haworth Press, Inc.) Vol. 13, No. 1/2 (#25/26), 2005, pp. 361-376; and: *Ecological Responses and Adaptations of Crops to Rising Atmospheric Carbon Dioxide* (ed: Zoltán Tuba) Food Products Press, an imprint of The Haworth Press, Inc., 2005, pp. 361-376. Single or multiple copies of this article are available for a fee from The Haworth Document Delivery Service [1-800-HAWORTH, 9:00 a.m. - 5:00 p.m. (EST). E-mail address: docdelivery@haworthpress.com].

<http://www.haworthpress.com/web/JCRIP>

© 2005 by The Haworth Press, Inc. All rights reserved.

Digital Object Identifier: 10.1300/J411v13n01\_17

361

## INTRODUCTION

The earth's atmospheric carbon dioxide concentration ( $[\text{CO}_2]$ ) has increased from a mean concentration of approximately 280 parts per million (ppm) since the start of the Industrial Revolution in Western Europe (1750-1800) to about 375 ppm at present. With the rapid increase in world population and economic activity, a doubling of the present atmospheric  $[\text{CO}_2]$  could be expected before the end of this century (Morison and Lawlor, 1999). As  $\text{CO}_2$  is responsible for about 61% of global warming (Shine et al., 1990), a doubling of the atmospheric  $[\text{CO}_2]$  and a rise in other "greenhouse" gases, including methane, chlorofluorocarbons, nitrous oxide and ozone, would increase the mean global air temperature, possibly by as much as  $6^\circ\text{C}$  (Morison and Lawlor, 1999; Schneider, 2001), and cause shifts in regional scale precipitation patterns that would result in unpredictable weather in many areas of the world (Wigley and Raper, 1992; Keeling et al., 1995).

Atmospheric  $\text{CO}_2$  is the basis for almost all life on earth. It is the primary raw material used by green plants to produce, through photosynthesis, the basic compounds out of which they construct their tissues and provide sustenance for other living things, ourselves included. Present understanding of photosynthetic carbon metabolism classifies terrestrial plants into three major photosynthetic categories:  $\text{C}_3$ ,  $\text{C}_4$ , and Crassulacean acid metabolism (CAM). Approximately 95% of terrestrial plant species fix atmospheric  $\text{CO}_2$  by the  $\text{C}_3$  photosynthetic pathway, while 1% fix  $\text{CO}_2$  by the  $\text{C}_4$  pathway and 4% by CAM (Bowes, 1993). Current atmospheric  $[\text{CO}_2]$  restricts the photosynthetic performance, growth and yield of many crop plants, most of which are  $\text{C}_3$ . Therefore, they are expected to respond to a greater extent to rising atmospheric  $[\text{CO}_2]$  than  $\text{C}_4$  and CAM species. The reason for such an expectation is that current atmospheric  $\text{CO}_2$  and  $\text{O}_2$  levels result in up to 40% photorespiratory losses in  $\text{C}_3$  plants (Matsuoka et al., 2001). Therefore, the assumption that a rise in atmospheric  $[\text{CO}_2]$  will reduce the deleterious effect of  $\text{O}_2$  on  $\text{C}_3$  photosynthesis has been supported by experimental research. Exposure of  $\text{C}_3$  plants to elevated growth  $[\text{CO}_2]$  generally results in stimulated photosynthesis and enhanced growth and yield (Kimball, 1993; Poorter et al., 1996; Drake et al., 1997). A compilation of the existing data available from the literature for  $\text{C}_3$  agricultural crop species indicates that a doubling of the present atmospheric  $[\text{CO}_2]$  would increase net photosynthetic rate up to 63%, and growth and yield up to 58% (Kimball, 1983, 1993; Poorter 1993; Poorter et al., 1996; Norby et al., 1999).

In this review, the responses of citrus photosynthesis, growth, and yield to rising atmospheric  $[\text{CO}_2]$  will be discussed. Comparisons will be made to research conducted on other crop species. Growth and development of citrus, as well as other agricultural crop species, are the results of many interacting pro-

cesses, including photosynthesis and its direct relationship to crop yield (Vu, 1999). In terms of photosynthesis, the  $\text{CO}_2$  exchange rate (CER) is dependent on a multitude of reactions, each with a potentially unique response to environmental factors (Sage and Reid, 1994). Rising atmospheric  $[\text{CO}_2]$  *per se* could benefit citrus, as well as many other economically important  $\text{C}_3$  species, but gains may or may not be realized in long-term growth due to the interaction of various adverse environmental factors that complicate the issue. As with other crop species, the ability of citrus to acclimate and/or compensate to rising atmospheric  $[\text{CO}_2]$  and other climate change factors is critical to its performance.

### **CITRUS PHOTOSYNTHESIS AT ELEVATED ATMOSPHERIC $\text{CO}_2$**

#### ***Photosynthetic Rates***

Leaf or whole-tree CER of a variety of citrus genotypes, when measured at the  $[\text{CO}_2]$  used for growth, is enhanced by elevated  $[\text{CO}_2]$  (Table 1, column 2) (Downton et al., 1987; Idso and Kimball, 1992b; Brakke and Allen, 1995; Syvertsen and Graham, 1999; Syvertsen et al., 2000; Jifon et al., 2002; Morinaga, 2002; Vu et al., 2002). In Valencia sweet orange, CER of both pre-existing leaves and new leaves is 16 to 98% higher at 800 ppm than at 400 ppm growth  $[\text{CO}_2]$  (Downton et al., 1987). In Ambersweet orange, the percentage enhancement in CER by double-ambient growth  $[\text{CO}_2]$  (720 ppm) is about 44% for the pre-existing mature leaves and 36% for the new young leaves (Figure 1A). Data collected over a three-year period on sour orange trees also show that the mean daylight photosynthetic rate of the leaves under summer conditions in Phoenix, Arizona (USA) is about 2.2-fold greater for the elevated (700 ppm)  $\text{CO}_2$  treatment in comparison with the near-ambient (400 ppm)  $\text{CO}_2$  treatment (Idso et al., 1991). Furthermore, leaf CER of several citrus genotypes commonly used as rootstocks in commercial citriculture, including lemon, citrange and mandarin, is enhanced up to 145% under elevated  $[\text{CO}_2]$  (from 720 to 840 ppm) (Brakke and Allen, 1995; Syvertsen et al., 2000).

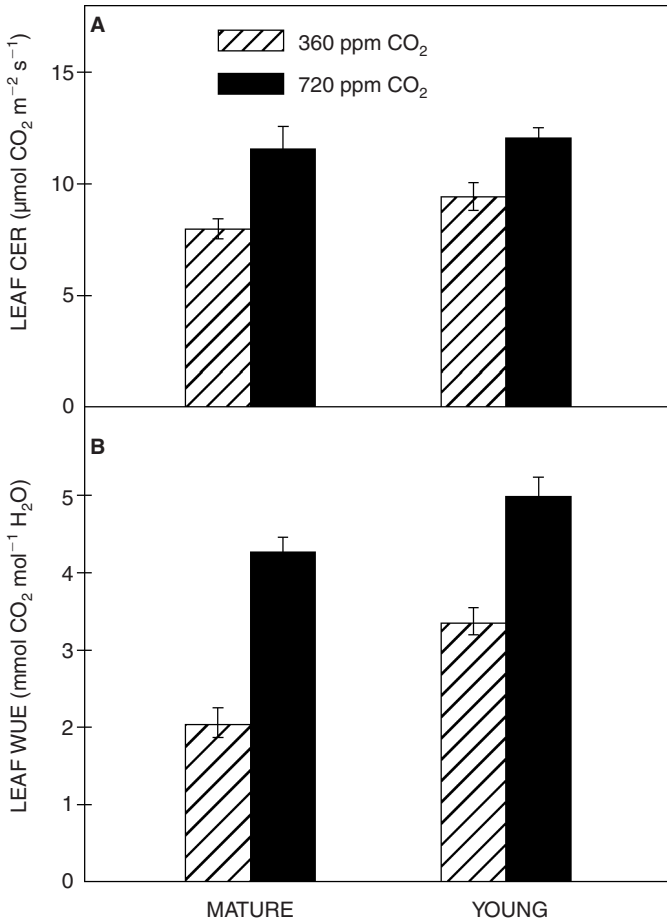
Although supraoptimum temperatures adversely affect photosynthesis of many crop plants (Morison and Lawlor, 1999), there has been an indication that elevated growth  $[\text{CO}_2]$  may partially alleviate the high temperature-stressed effects on leaf photosynthetic rate (Long, 1991). This arises from the fact that photorespiration rates increase at higher air temperatures under current atmospheric  $\text{CO}_2$  levels, but significantly decrease at elevated  $[\text{CO}_2]$ . Theoretically, a 300-ppm increase in growth  $[\text{CO}_2]$  could raise the temperature optimum of light-saturated CER of  $\text{C}_3$  plants by  $5^\circ\text{C}$  (Long, 1991). Photo-

TABLE 1. Percent enhancement in photosynthesis (CER), growth parameters and fruit yield of various citrus genotypes by double-ambient growth [CO<sub>2</sub>].

Citrus Genotypes	% Enhancement in CER	% Enhancement in Growth/Fruit
'Ambersweet' orange (Allen and Vu, 2000; Vu et al., 2002)	36-44	17-49 (specific leaf weight) 15-37 (total tree biomass)
'Ridge Pineapple' sweet orange (Jifon et al., 2002)	55-75	45 (total tree biomass)
'Valencia' sweet orange (Downton et al., 1987)	16-98	25 (specific leaf weight) 70 (fruit)
Sour orange (Idso et al., 1991; Idso and Kimball, 1992,1997)	~120	79 (leaves) 56-240 (branches) 70-2400 (fruit)
Sour orange (Jifon et al., 2002)	36-102	58 (total tree biomass)
'Carrizo' citrange (Brakke and Allen, 1995 Koch et al., 1986,1987)	~100	67-120 (total tree biomass)
'Swingle' citrumelo (Koch et al., 1986)	~100	115 (total tree biomass)
'Cleopatra' mandarin (Syvertsen et al., 2000)	13-37	23-33 (specific leaf weight)
'Troyer' citrange (Syvertsen et al., 2000)	72-145	31-34 (specific leaf weight)
'Volkamer' lemon (Syvertsen et al., 2000)	31-44	13-52 (specific leaf weight)

synthesis measurements made during four consecutive summers for sour orange trees grown outdoors at Phoenix, Arizona show that there is a negative linear relationship between leaf CER and leaf temperature from 31 to 47°C for both ambient and elevated CO<sub>2</sub>-grown trees, indicating that this temperature range is above the optimum for net photosynthesis of this citrus species (Idso et al., 1995). Under hot and dry summer conditions in Phoenix, leaf CER of sour orange trees is highest (about 6 and 11  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for ambient and elevated CO<sub>2</sub>-grown trees, respectively) at the morning's first measurements at 7:00 a.m. (31°C), and steadily declines thereafter. By 2:00 p.m. (47°C), leaf CER of the ambient CO<sub>2</sub>-grown sour orange trees drops to near zero, whereas the CO<sub>2</sub>-enriched trees still maintain their leaf photosynthetic rate at a sub-

FIGURE 1. Midday  $\text{CO}_2$  exchange rate (CER) (A) and water-use efficiency (WUE) (B) of pre-existing mature leaves and new young leaves of Ambersweet orange trees grown for 29 months under 360 and 720 ppm  $\text{CO}_2$ . Each data value represents the mean (with SE bar) of 8 to 10 determinations.



stantially high level ( $\sim 4 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) (Idso et al., 1991, 1995). Nevertheless, the degree of CER enhancement in sour orange by  $\text{CO}_2$  enrichment is 75% at a leaf temperature of  $31^\circ\text{C}$ , 100% at  $35^\circ\text{C}$ , and 200% at  $42^\circ\text{C}$ . Similar scenarios, although to a lesser extent, have been reported for soybean (Vu et al., 1997). The enhancements in sour orange leaf CER by elevated  $[\text{CO}_2]$  fall in the range of the predictions for an idealized  $\text{C}_3$  plant, showing that a rise in temperature

from 28 to 40°C increases CER enhancement from 66 to 190% when growth [CO<sub>2</sub>] is raised from 350 to 650 ppm (Long, 1991). In Ambersweet orange, there is a small and consistent, although not significant, increase in CER at growth temperature of about 6°C above ambient temperature for both pre-existing mature and new young leaves at double-ambient growth [CO<sub>2</sub>] (Vu et al., 2002). This indicates that for citrus there are genotype-specific differences in leaf CER responses to elevated growth CO<sub>2</sub> and temperature. In addition, differences in experimental and environmental growth conditions, CO<sub>2</sub> enrichment levels, leaf/tree growth stages used for the measurements, as well as time of the day when CER measurements were carried out, all of these would also contribute to the reported differences on CER and enhancements in CER by high [CO<sub>2</sub>] and temperature.

Citrus responds, as do other reported herbaceous and woody species, to elevated atmospheric [CO<sub>2</sub>] with a decrease in stomatal conductance, resulting in a reduction in leaf transpiration and consequently an improvement in leaf water-use efficiency (WUE), the ratio of leaf CER to leaf transpiration rate (Syvertsen and Graham, 1999; Syvertsen et al., 2000; Vu et al, 2002). However, the magnitude of stomatal response to elevated [CO<sub>2</sub>] is species-specific and is generally smaller in trees than in annual crops (Field et al., 1995; Norby et al., 1999). In Ambersweet orange, stomatal conductance of pre-existing mature leaves of trees grown for more than two years at double-ambient [CO<sub>2</sub>] is about 32% lower than their counterparts at ambient [CO<sub>2</sub>] (Vu et al., 2002). WUE of the elevated CO<sub>2</sub>-grown sweet orange trees is 105% greater for mature leaves and 47% higher for young leaves at near-ambient temperature (Figure 1B). Such enhancements in leaf WUE under elevated growth [CO<sub>2</sub>] are even larger at growth temperature of 4.5°C above ambient: 150 and 94% for mature and young leaves, respectively (Vu et al., 2002).

In addition to a potential increase in mean global air temperature, shifts in regional precipitation patterns as a result of rising atmospheric [CO<sub>2</sub>] will probably decrease soil water availability in many areas of the world. Soil water deficit, or drought, is the single most important factor limiting crop growth and yield (Hsiao, 1973). Production of agricultural crops, including citrus, in semiarid and arid areas of the world depends heavily on irrigation (Yelenosky, 1991; Vu, 1999). Even in normally humid areas, irrigation systems are installed to prevent yield reduction due to short dry periods. For citrus, as well as many other crops, an increase in drought stress is followed by decreasing CER, and such a reduction has been partially attributed to stomatal closure (Vu and Yelenosky, 1988; Vu et al., 1998; Vu, 1999). In Valencia sweet orange, drought stress also reduces photosynthetic carboxylating enzyme activity and protein concentration and shifts carbohydrate distribution in the leaves (Vu and Yelenosky, 1988, 1989). Unfortunately, not much is known about the

interactive nature of rising atmospheric  $[\text{CO}_2]$  and drought on photosynthesis and growth of citrus.

### ***Leaf Photosynthetic Biochemistry***

Long-term exposure of  $\text{C}_3$  plants to elevated  $[\text{CO}_2]$  leads to a variety of acclimation effects, including changes in leaf photosynthetic physiology and biochemistry, and alterations in morphology, anatomy, branching, tillering, timing of developmental events and life cycle completion (Bowes, 1993; Drake et al., 1997). A greater number of mesophyll cells and chloroplasts have been reported for a variety of plants grown at elevated  $[\text{CO}_2]$  (Thomas and Harvey, 1983; Vu et al., 1989). In terms of leaf photosynthetic physiology and biochemistry, acclimation occurs, ranging from species-specific changes in the CER versus intercellular  $\text{CO}_2$  response curves (Radin et al., 1987; Campbell et al., 1988; Sage et al., 1989) to alterations in dark respiration (Drake et al., 1997) and enzyme biochemistry, especially ribulose biphosphate carboxylase-oxygenase (Rubisco) (Bowes, 1996). Many  $\text{C}_3$  species grown for long periods at elevated  $[\text{CO}_2]$  show a decrease in leaf photosynthesis (Sage et al., 1989; Besford et al., 1990). In addition, carbohydrate source-sink imbalance under growth at elevated  $[\text{CO}_2]$  is believed to have a major role in the regulation of photosynthesis through feedback inhibition (Arp, 1991; Stitt, 1991; Makino and Mae, 1999).

The photosynthetic carboxylating enzyme Rubisco "fixes" atmospheric  $\text{CO}_2$  and thus plays a vital role in plant growth and productivity. Activity of Rubisco, concentration of the Rubisco protein, and the level of the Rubisco small subunit transcript (*rbcS*) have been frequently used as indicators/markers to evaluate the acclimation of leaf photosynthetic capacity at elevated growth  $[\text{CO}_2]$ . For many  $\text{C}_3$  crops including sweet orange, longer exposure to elevated  $[\text{CO}_2]$  results in a down-regulation of Rubisco activity (Wong, 1979; Vu et al., 1983; Sage et al., 1989; Bowes, 1996; Drake et al., 1997; Vu et al., 1983, 1997, 2002). In addition, elevated  $[\text{CO}_2]$  affects the relative expression of the Rubisco protein concentration and its transcript levels in a variety of plant species (Gesch et al., 1998; Moore et al., 1998, 1999; Vu et al., 1999, 2001). Under long-term elevated growth  $[\text{CO}_2]$ , some plants show reductions in both Rubisco protein content and *rbcS* abundance, whereas others show decreases in the Rubisco protein but not in the *rbcS* transcript (Moore et al., 1998). In Ambersweet orange, reductions in the Rubisco protein content at a double-ambient growth  $[\text{CO}_2]$  are substantial (Vu et al., 2002), but attempts to characterize the *rbcS* message levels were unsuccessful. Although no correlation between Rubisco protein content and *rbcS* mRNA abundance was made for sweet orange, total RNA levels in trees grown at double-ambient  $[\text{CO}_2]$



were 38-49% less for pre-existing mature leaves, and 19-31% less for young leaves (Vu, unpublished data).

In Ambersweet orange, down-regulation of the Rubisco protein concentration under elevated growth  $[\text{CO}_2]$  does not entail a change in the level of total leaf soluble protein (Vu et al., 2002). New young leaves contain a similar amount of total soluble protein as pre-existing mature leaves, regardless of the growth  $[\text{CO}_2]$ . In sour orange, however, leaf soluble proteins show some decrease in concentration in new young leaves from trees grown at elevated  $[\text{CO}_2]$  (Weber et al., 1994). The decline in Rubisco protein concentration without a reduction in total soluble protein content in Ambersweet orange at elevated growth  $[\text{CO}_2]$ , however, would allow an optimization of nitrogen use, either by reallocating the nitrogen resources away from Rubisco to other proteins within the leaves, or redistributing nitrogen from the photosynthetic proteins of source leaves to sink tissues (Stitt, 1991; Bowes, 1993).

For citrus, the reduction in activity and/or protein concentration of Rubisco at elevated growth  $[\text{CO}_2]$  may be genotype-specific, since Rubisco activity has been reported to be greater for Swingle citrumelo grown at twice ambient  $[\text{CO}_2]$ , but not in leaf samples from Carrizo citrange (Koch et al., 1986). However, Rubisco activity for these two citrus rootstocks was expressed on a leaf chlorophyll basis, and not on a leaf area basis as for Rubisco activity of Ambersweet orange (Vu et al., 2002). Therefore, claims that Rubisco is modulated by elevated growth  $[\text{CO}_2]$  requires more careful evaluation, as the basis on which activity and/or concentration of the enzyme are expressed may vary or nullify observations (Bowes, 1993).

In addition to Rubisco, other proteins may be considered as photosynthetic genes, but available information on their responses to elevated growth  $[\text{CO}_2]$  is limited. In tomato, mRNA levels of Rubisco activase decline under elevated  $[\text{CO}_2]$  (van Oosten et al., 1994). Activity and mRNA levels of carbonic anhydrase, the enzyme facilitating diffusion of  $\text{CO}_2$  from intercellular air spaces, are reduced in some plant species, but unchanged or even increased in the others (Moore et al., 1999). Activities of sucrose phosphate synthase (SPS) and acid invertase and adenosine 5'-diphosphoglucose pyrophosphorylase (ADGP), the enzymes involving in sucrose and starch metabolism, respectively, may be affected by elevated growth  $[\text{CO}_2]$ . However, the responses of these enzymes to elevated  $[\text{CO}_2]$  are also species-specific. In rice, leaf SPS activity is enhanced in  $\text{CO}_2$ -enriched plants, suggesting an acclimation response to optimize the capacity for carbon utilization and export for this crop (Hussain et al., 1999). On the other hand, activity of SPS is down-regulated by elevated  $[\text{CO}_2]$  in bean, cotton, cucumber, plantain and wheat, but up-regulated in pea, soybean, spinach, sunflower and tomato (Moore et al., 1998). Under elevated growth  $[\text{CO}_2]$ , leaf acid invertase activity is down-regulated in cotton, cucumber, parsley, pea, radish, soybean, spinach, tobacco, and wheat,

but up-regulated in bean, plantain, and sunflower (Moore et al., 1998). In Ambersweet orange grown under elevated  $[\text{CO}_2]$ , activities of SPS and ADGP are down-regulated in the pre-existing mature leaves, but not in the new young leaves (Vu et al., 2002).

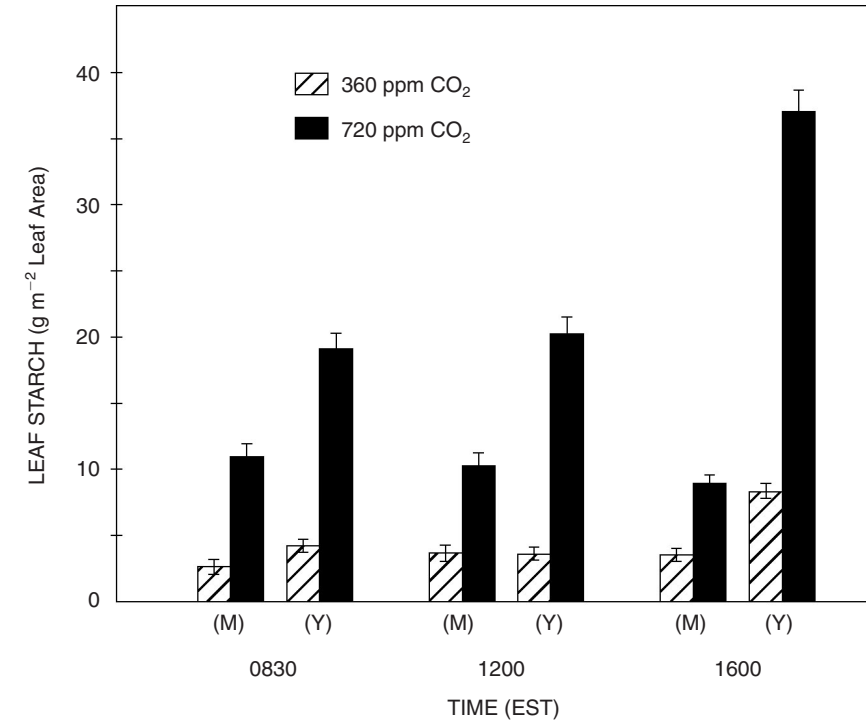
In sour orange grown at elevated  $[\text{CO}_2]$ , concentrations of glucose, fructose, and sucrose in the new leaves are more than three-fold those of ambient- $[\text{CO}_2]$  controls (Weber et al., 1994). In Ambersweet orange, the levels of foliar nonstructural carbohydrates are substantially higher in midday-sampled leaves of trees grown at double-ambient  $[\text{CO}_2]$  than their counterparts at ambient  $[\text{CO}_2]$ . At double-ambient  $[\text{CO}_2]$ , glucose is increased up to 115%, fructose up to 164%, sucrose up to 73%, total soluble sugars up to 50%, starch up to 424%, and total nonstructural carbohydrates up to 166% (Vu et al., 2002). Diurnal leaf sampling analyses show that starch contents of both pre-existing mature and new young leaves of Ambersweet orange are several-fold higher under double-ambient growth  $[\text{CO}_2]$  (Figure 2). Particularly for new young leaves, starch content of the  $\text{CO}_2$ -enriched trees at late afternoon sampling is more than four-fold greater than their counterparts at ambient  $[\text{CO}_2]$ . For sour orange and sweet orange, growth at elevated  $[\text{CO}_2]$  (700 ppm) significantly increases starch content in leaves and fibrous roots (Jifon et al., 2002). Despite the large accumulation of leaf starch that often occurs at elevated growth  $[\text{CO}_2]$  for several crop plants, there is report that the levels of mRNA for ADPG shows little change (van Oosten et al., 1994).

### **CITRUS GROWTH AND YIELD AT ELEVATED ATMOSPHERIC $\text{CO}_2$**

Growth of a variety of citrus genotypes, including sweet orange, sour orange, citrange and citrumelo, appears to be as responsive as that of several other annual crop species to elevated  $[\text{CO}_2]$  (Table 1, column 3) (Koch et al., 1986, 1987; Baker and Allen, 1993; Idso et al., 1991; Idso and Kimball, 1997, 2001; Syvertsen and Graham, 1999; Syvertsen et al., 2000; Jifon et al., 2002). Fourteen-week-old seedlings of Carrizo citrange and Swingle citrumelo grown for 5 months under double-ambient  $[\text{CO}_2]$  have 69 to 94% more new shoots, total shoot dry weight increased by over 100%, total leaf area increased by 85 to 124% due to greater leaf number and size, total root dry weight increased by 37 to 100%, and total dry matter accumulation increased by 111 to 115% (Koch et al., 1986). In a subsequent experiment, exposure of 9-week-old seedlings of Carrizo citrange to double-and triple-ambient  $[\text{CO}_2]$  for 17 weeks enhances total dry matter by 67 and 120%, respectively (Koch et al., 1987).

A long-term atmospheric  $\text{CO}_2$  enrichment study on growth and fruit production of sour orange trees was conducted outdoors, in clear-plastic wall

FIGURE 2. Diurnal changes in starch levels of pre-existing mature leaves (M) and new young leaves (Y) of Ambersweet orange trees grown for 29 months under 360 and 720 ppm CO<sub>2</sub>. Each data value represents the mean (with SE bar) of 4 determinations.



open-top chambers, at Phoenix, Arizona (Idso et al., 1991). Identical seedlings of sour orange, which had been grown outdoors and rooted in the ground, were half maintained at near-ambient [CO<sub>2</sub>] (400 ppm) and half at 300 ppm above ambient (CO<sub>2</sub>-enriched). In less than two years, the trunks of the CO<sub>2</sub>-enriched trees are twice as large as their ambient-CO<sub>2</sub> treatment counterparts. By the end of the second year, the CO<sub>2</sub>-enriched trees had 79% more leaves, 56% more primary branches, 70% more secondary branches, 240% more tertiary branches, and 279% more total trunk plus branch volume than the ambient-CO<sub>2</sub> trees (Idso et al., 1991; Idso and Kimball, 1992a). Three years later, the trunk plus branch volume factor of the CO<sub>2</sub>-enriched trees was still about 200% that of the ambient-CO<sub>2</sub> trees (Idso and Kimball, 1997). These results, when compared with CO<sub>2</sub> enrichment studies on annual C<sub>3</sub> crops (Kimball,

1983), suggest that the perennial citrus species may respond proportionally more strongly to rising atmospheric  $[\text{CO}_2]$  than several other annual plant species. Fruit harvests during a six consecutive year period (years 3 to 8) for sour orange show that the average numbers of fruits produced per tree for the  $\text{CO}_2$ -enriched treatment are 25.0-, 6.9-, 3.6-, 2.3-, 2.0- and 1.7-fold those produced per tree for the ambient- $\text{CO}_2$  treatment (Idso and Kimball, 1997). Although not significantly different, the mean volume of the  $\text{CO}_2$ -enriched fruits is about 4% larger than that of the ambient- $\text{CO}_2$  treatment fruits. Over the first two years of this on-going study, elevated growth  $[\text{CO}_2]$  caused the  $\text{CO}_2$ -enriched/ambient-treatment ratio of the tree aboveground wood biomass to rise to a value in excess of 3.0, but gradually declined thereafter to level out at about 1.8 at the end of seven more years. Similarly, the ratio of yearly fruit biomass production of the  $\text{CO}_2$ -enriched/ambient-treatment over the last four years (years 10-13) also maintained the same average and essentially identical value as the aboveground wood biomass ratio (Idso and Kimball, 2001). This indicates that the  $\text{CO}_2$ -enriched sour orange trees may have reached by year 8-10 an equilibrium condition in terms of  $\text{CO}_2$ -induced enhancements in wood biomass and fruit production, and such steady-state responses likely will be maintained over the remainder of their lifespan (Idso and Kimball, 2001).

Downton et al. (1987) conducted experiments on yield response to elevated  $[\text{CO}_2]$  of 3-year-old Valencia sweet orange trees over a 12-month period. Trees grown under enriched (800 ppm)  $[\text{CO}_2]$  produce 70% more fruit, although similar in size and weight to that of control trees grown at 400 ppm  $[\text{CO}_2]$ . In their study, although leaf areas between treatments are similar, specific leaf dry weight is 25% greater for the  $\text{CO}_2$ -enriched trees. In Ambersweet orange, double-ambient growth  $[\text{CO}_2]$  treatment over a 29-month period does not significantly affect leaf area, but increases specific leaf weight 17 to 23% for pre-existing mature leaves, and 19 to 49% for young leaves (Vu et al., 2002). Dry weight response ratios to growth  $\text{CO}_2$  (elevated/ambient) for the first year are 1.01 for leaves, 1.57 for shoot wood, 1.40 for roots, and 1.37 for total tree. At the end of the second year, the ratios are 1.05 for leaves, 1.20 for shoot wood, 1.15 for roots, and 1.15 for total tree (Allen and Vu, 2000). The large decrease in Ambersweet orange response to elevated  $[\text{CO}_2]$  in the second year is attributed to crowding of shoot and root space. As for the differences in  $\text{CO}_2$  enhancements on citrus photosynthetic rate (Table 1, column 2), the variations in citrus growth and yield responses to elevated growth  $[\text{CO}_2]$  (Table 1, column 3) also indicate that, among citrus, genotype-specific differences will be encountered as a result of future increases in global  $[\text{CO}_2]$  and air temperatures. Besides, differences in growth and environment conditions as well as levels and durations of  $\text{CO}_2$  treatments during the experimental periods would definitely contribute to reported variations in citrus growth and yield responses to  $\text{CO}_2$  enrichment.

## CONCLUDING REMARKS

Citrus, with its high value for nutritional and palatable qualities, enters the 21st century as one of the most important fruit crops in world trade (Vu, 1999). Sizable increases in yield of citrus could be anticipated in response to future rises in global atmospheric  $[\text{CO}_2]$ , but expected climate changes as induced by rising  $[\text{CO}_2]$  and other greenhouse gases could have severe adverse impacts. Rising atmospheric  $[\text{CO}_2]$  and potential climate changes critically challenge our needs in understanding the mechanisms and processes directing citrus growth and yield. There is merit in the concept that "the superior genetically engineered citrus tree will ultimately provide the long-term solutions to environmental stresses" (Yelenosky, 1991). It is imperative therefore that citrus environmental stress research continues unabated with the eventual result of increased growth and yield under future global climate changes.

## REFERENCES

- Allen, L.H., Jr., and J.C.V. Vu. (2000). Carbon dioxide and temperature effects on young sweet orange trees. 2000 Annual Meetings Abstracts. American Society of Agronomy, November 5-9, Minneapolis, Minnesota, p. 34.
- Arp, W.J. (1991). Effects of source-sink relations on photosynthetic acclimation to  $\text{CO}_2$ . *Plant, Cell and Environment* 14: 869-875.
- Baker, J.T., and L.H. Allen, Jr. (1993). Contrasting crop species responses to  $\text{CO}_2$  and temperature: rice, soybean and citrus. *Vegetatio* 104/105: 239-260.
- Besford, R.T., L.J. Ludwig, and A.C. Withers. (1990). The greenhouse effect: acclimation of tomato plants growing in high  $\text{CO}_2$ , photosynthesis and ribulose-1,5-bisphosphate carboxylase protein. *Journal of Experimental Botany* 41: 925-931.
- Bowes, G. (1993). Facing the inevitable: Plants and increasing atmospheric  $\text{CO}_2$ . *Annual Review of Plant Physiology and Plant Molecular Biology* 44: 309-332.
- Bowes, G. (1996). Photosynthetic responses to changing atmospheric carbon dioxide concentration. In *Photosynthesis and the Environment*, ed. N.R. Baker. Dordrecht: Kluwer Academic Publishers, pp. 387-407.
- Brakke, M., and L.H. Allen Jr. (1995). Gas exchange of *Citrus* seedlings at different temperatures, vapor-pressure deficits, and soil water contents. *Journal of the American Society for Horticultural Science* 120: 497-504.
- Campbell, W.J., L.H. Allen Jr., and G. Bowes. (1988). Effects of  $\text{CO}_2$  concentration on rubisco activity, amount, and photosynthesis in soybean leaves. *Plant Physiology* 88: 1310-1316.
- Downton, W.J.S., W.J.R. Grant, and B.R. Loveys. (1987). Carbon dioxide enrichment increases yield of Valencia orange. *Australian Journal of Plant Physiology* 14: 493-501.
- Drake, B.G., M.A. Gonzalez-Meler, and S.P. Long. (1997). More efficient plants: A consequence of rising atmospheric  $\text{CO}_2$ ? *Annual Review of Plant Physiology and Plant Molecular Biology* 48: 609-639.

- Field, C.B., R.B. Jackson, and H.A. Mooney. (1995). Stomatal responses to increased CO<sub>2</sub>: implications from the plant to the global scale. *Plant, Cell and Environment* 18: 1214-1225.
- Gesch, R.W., K.J. Boote, J.C.V. Vu, L.H. Allen Jr., and G. Bowes. (1998). Changes in growth CO<sub>2</sub> result in rapid adjustments of ribulose-1,5-bisphosphate carboxylase/oxygenase small subunit gene expression in expanding and mature leaves of rice. *Plant Physiology* 118: 521-529.
- Hsiao, T.C. (1973). Plant responses to water stress. *Annual Review of Plant Physiology* 24: 519-570.
- Hussain, M.W., L.H. Allen Jr., and G. Bowes. (1999). Up-regulation of sucrose phosphate synthase in rice grown under elevated CO<sub>2</sub> and temperature. *Photosynthesis Research* 60: 199-208.
- Idso, S.B., B.A. Kimball, and S.G. Allen. (1991). CO<sub>2</sub> enrichment of sour orange trees: 2.5 years into a long-term experiment. *Plant, Cell and Environment* 14: 351-353.
- Idso, S.B., and B.A. Kimball. (1992a). Aboveground inventory of sour orange trees exposed to different atmospheric CO<sub>2</sub> concentrations for 3 full years. *Agricultural and Forest Meteorology* 60: 145-151.
- Idso, S.B., and B.A. Kimball. (1992b). Effects of atmospheric CO<sub>2</sub> enrichment on photosynthesis, respiration, and growth of sour orange. *Plant Physiology* 99: 341-343.
- Idso, S.B., K.E. Idso, R.L. Garcia, B.A. Kimball, and J.K. Hooper. (1995). Effects of atmospheric CO<sub>2</sub> enrichment and foliar methanol application on net photosynthesis of sour orange tree (*Citrus aurantium*; Rutaceae) leaves. *American Journal of Botany* 82: 26-30.
- Idso, S.B., and B.A. Kimball. (1997). Effects of long-term atmospheric CO<sub>2</sub> enrichment on the growth and fruit production of sour orange trees. *Global Change Biology* 3: 89-96.
- Idso, S.B., and B.A. Kimball. (2001). CO<sub>2</sub> enrichment of sour orange trees: 13 years and counting. *Environmental and Experimental Botany* 46: 147-153.
- Jifon, J.L., J.H. Graham, D.L. Drouillard, and J.P. Syvertsen. (2002). Growth depression of mycorrhizal *Citrus* seedlings grown at high phosphorus supply is mitigated by elevated CO<sub>2</sub>. *New Phytologist* 153: 133-142.
- Keeling, C.D., T.P. Whorf, M. Wahlen, and J. van der Plicht. (1995). Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* 375: 660-670.
- Kimball, B.A. (1983). Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. *Agronomy Journal* 75: 779-788.
- Kimball, B.A. (1993). Effects of elevated CO<sub>2</sub> and climate variables on plants. *Journal of Soil and Water Conservation* 48: 9-14.
- Koch, K.E., P.H. Jones, W.T. Avigne, and L.H. Allen Jr. (1986). Growth, dry matter partitioning, and diurnal activities of RuBP carboxylase in citrus seedlings maintained at two levels of CO<sub>2</sub>. *Physiologia Plantarum* 67: 477-484.
- Koch, K.E., L.H. Allen Jr., P. Jones, and W.T. Avigne. (1987). Growth of citrus rootstock (Carrizo Citrange) seedlings during and after long-term CO<sub>2</sub> enrichment. *Journal of the American Society for Horticultural Science* 112: 77-82.

- Long, S.P. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO<sub>2</sub> concentrations: has its importance been underestimated? *Plant, Cell and Environment* 14: 729-739.
- Makino, A., and T. Mae. (1999). Photosynthesis and plant growth at elevated levels of CO<sub>2</sub>. *Plant, Cell and Environment* 40: 999-1006.
- Matsuoka, M., R.T. Furbank, H. Fufayama, and M. Miyao. (2001). Molecular engineering of C<sub>4</sub> photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 52: 297-314.
- Moore, B.D., S-H. Cheng, and J.R. Seemann. (1998). Sucrose cycling, Rubisco expression, and prediction of photosynthetic acclimation to elevated atmospheric CO<sub>2</sub>. *Plant, Cell and Environment* 21: 905-915.
- Moore, B.D., S-H. Cheng, D. Sims, and J.R. Seemann. (1999). The biochemical and molecular basis for photosynthetic acclimation to elevated atmospheric CO<sub>2</sub>. *Plant, Cell and Environment* 22: 567-582.
- Morinaga, K. (2002). Effects of fruit load on photosynthesis and ribulose 1,5-bisphosphate carboxylase activity in satsuma mandarin (*Citrus unshiu* Marc.) trees under long-term elevated carbon dioxide. *Journal of the Japanese Society for Horticultural Science* 71: 311-316.
- Morison, J.I.L., and D.W. Lawlor. (1999). Interactions between increasing CO<sub>2</sub> concentration and temperature on plant growth. *Plant, Cell and Environment* 22: 659-682.
- Norby, R.J., S.D. Wullschleger, C.A. Gunderson, D.W. Johnson, and R. Ceulemans. (1999). Tree responses to rising CO<sub>2</sub> in the field experiments: implications for the future forest. *Plant, Cell and Environment* 22: 683-714.
- Poorter, H. (1993). Interspecific variation in the grown response of plants to an elevated ambient CO<sub>2</sub> concentration. *Vegetatio* 104/105: 77-97.
- Poorter, H., C. Roumet, and B.D. Campbell. (1996). Interspecific variation in the growth response of plants to elevated CO<sub>2</sub>: A search for functional types. In *Carbon Dioxide, Populations, and Communities*, ed. C. Körner, and F.A. Bazzaz. Academic Press, New York, pp. 375-412.
- Radin, J.W., B.A. Kimball, D.L. Hendrix, and J.R. Mauney. (1987). Photosynthesis of cotton plants exposed to elevated levels of carbon dioxide in the field. *Photosynthesis Research* 12: 191-203.
- Sage, R.F., T.D. Sharkey, and J.R. Seemann. (1989). Acclimation of photosynthesis to elevated CO<sub>2</sub> in five C<sub>3</sub> species. *Plant Physiology* 89: 590-596.
- Sage, R.F., and C.D. Reid. (1994). Photosynthetic response mechanisms to environmental change in C<sub>3</sub> plants. In *Plant-Environment Interactions*, ed. R.E. Wilkinson. Marcel Dekker, Inc., New York, pp. 413-499.
- Schneider, S.H. (2001). What is "dangerous" climate change? *Nature* 411: 17-19.
- Shine, K.P., R.G. Derwent, D.J. Wuebbles, and J.J. Morcrette. (1990). Radiative forcing of climate. In *Climatic Change. The IPCC Scientific Assessment*, ed. J.T. Houghton, G.J. Jenkins, and J.J. Ephraums. Cambridge University Press, Cambridge, pp. 41-68.
- Stitt, M. (1991). Rising CO<sub>2</sub> levels and their potential significance for carbon flow in photosynthetic cells. *Plant, Cell and Environment* 14: 741-762.



- Syverson, J.P., and J.H. Graham. (1999). Phosphorus supply and arbuscular mycorrhizas increase growth and net gas exchange responses of two *Citrus* spp. grown at elevated  $[\text{CO}_2]$ . *Plant and Soil* 208: 209-219.
- Syverson, J.P., L.S. Lee, and J.W. Grosser. (2000). Limitations on growth and net gas exchange of diploid and tetraploid *Citrus* rootstock cultivars grown at elevated  $\text{CO}_2$ . *Journal of the American Society for Horticultural Science* 125: 228-234.
- Thomas, J.F., and C.N. Harvey. (1983). Leaf anatomy of four species grown under continuous  $\text{CO}_2$  enrichment. *Botanical Gazette* 144: 303-309.
- van Oosten, J.-J., D. Wilkins, and R.T. Besford. (1994). Regulation of the expression of photosynthetic nuclear genes by high  $\text{CO}_2$  is mimicked by carbohydrates: a mechanism for the acclimation of photosynthesis to high  $\text{CO}_2$ . *Plant, Cell and Environment* 17: 913-923.
- Vu, C.V., L.H. Allen Jr., and G. Bowes. (1983). Effects of light and elevated atmospheric  $\text{CO}_2$  on the ribulose biphosphate carboxylase activity and ribulose biphosphate level of soybean leaves. *Plant Physiology* 73: 729-734.
- Vu, J.C.V., and G. Yelenosky. (1988). Water deficit and associated changes in some photosynthetic parameters in leaves of 'Valencia' orange (*Citrus sinensis* [L.] Osbeck). *Plant Physiology* 88: 375-378.
- Vu, J.C.V., and G. Yelenosky. (1989). Non-structural carbohydrate concentrations on leaves of 'Valencia' orange subjected to water deficits. *Environmental and Experimental Botany* 29: 149-154.
- Vu, J.C.V., L.H. Allen Jr., and G. Bowes. (1989). Leaf ultrastructure, carbohydrates and protein of soybeans grown under  $\text{CO}_2$  enrichment. *Environmental and Experimental Botany* 29: 141-147.
- Vu, J.C.V., L.H. Allen Jr., K.J. Boote, and G. Bowes. (1997). Effects of elevated  $\text{CO}_2$  and temperature on photosynthesis and Rubisco in rice and soybean. *Plant, Cell and Environment* 20: 68-76.
- Vu, J.C.V., J.T. Baker, A.H. Pennanen, L.H. Allen, Jr., G. Bowes, and K.J. Boote. (1998). Elevated  $\text{CO}_2$  and water deficit effects on photosynthesis, ribulose biphosphate carboxylase-oxygenase, and carbohydrate metabolism in rice. *Physiologia Plantarum* 103: 327-339.
- Vu, J.C.V. (1999). Photosynthetic responses of citrus to environmental changes. In *Handbook of Plant and Crop Stress*, ed. M. Pessarakli, Marcel Dekker, Inc., New York, pp. 947-961.
- Vu, J.C.V., R.W. Gesch, L.H. Allen, Jr., K.J. Boote, and G. Bowes. (1999).  $\text{CO}_2$  enrichment delays a rapid, drought-induced decrease in Rubisco small subunit transcript abundance. *Journal of Plant Physiology* 155: 139-142.
- Vu, J.C.V., R.W. Gesch, A.H. Pennanen, L.H. Allen, Jr., K.J. Boote, and G. Bowes. (2001). Soybean photosynthesis, Rubisco, and carbohydrate enzymes function at supraoptimal temperatures in elevated  $\text{CO}_2$ . *Journal of Plant Physiology* 158: 295-307.
- Vu, J.C.V., Y.C. Newman, L.H. Allen Jr., M. Gallo-Meagher, and M-Q. Zhang. (2002). Photosynthetic acclimation of young sweet orange trees to elevated growth  $\text{CO}_2$  and temperature. *Journal of Plant Physiology* 159: 147-157.
- Webber, A.N., G-Y. Nie, and S.P. Long. (1994). Acclimation of photosynthetic proteins to rising atmospheric  $\text{CO}_2$ . *Photosynthesis Research* 39: 413-425.



- Wigley, T.M.L., and S.C.B. Raper. (1992). Implications for climate and sea level of revised IPCC emissions scenarios. *Nature* 357: 293-300.
- Wong, S.C. (1979). Elevated atmospheric partial pressure of CO<sub>2</sub> and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C<sub>3</sub> and C<sub>4</sub> plants. *Oecologia* 44: 68-74.
- Yelenosky, G. (1991). Responses and adaptations of citrus trees to environmental stresses. *Israel Journal of Botany* 40: 239-250.